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Chromosomes of Philippine mammals (Insectivora, Dermoptera, Primates, Rodentia, Carnivora)

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Abstract.—Karyotypes of nine species of Philippine mammals representing five orders are presented. Chromosomes of six species are described for the first time, including three endemic insectivores (*Podogymnura truei, Crocidura beatus, C. grayi*), the endemic dermopteran (*Cynocephalus volans*), an endemic squirrel (*Sundasciurus philippinensis*), and a widespread viverrid (*Viverra tangalunga*). Some species endemic to the oceanic Philippines have unique karyotypes whereas other endemics and widespread Asian species have karyotypes that are similar, or identical, to those of related species or conspecifics occurring outside the archipelago. These data corroborate patterns of karyotype variation previously documented for Philippine bats and murid rodents.

For more than a century, the terrestrial mammal fauna of the Philippines has been recognized as a unique assemblage (Thomas 1898). All portions of this remarkable fauna, which includes 179 species representing nine orders, are characterized by a high proportion of endemic species. More than 60% of the mammal fauna, as a whole, is endemic (Heaney et al. 1998). For bats and murid rodents, the two largest faunal components, cytogenetic studies have provided insight into how these groups have diversified within the archipelago (Rickart et al. 1989, Rickart & Musser 1993, Rickart et al. 1999, Rickart & Heaney 2002). These studies suggest that chromosomal data on other Philippine taxa may help clarify their phylogenetic and biogeographic relationships. Accordingly, this report presents karyotypes of nine species representing five orders (Insectivora, Dermoptera, Primates, Rodentia, and Carnivora).

Methods

Specimens were collected during field studies conducted in 1987 (on Leyte, Biliran and Negros islands), 1988 (Luzon Island), and 1993 (Mindanao Island). Live-trapped animals were processed and killed with sodium pentobarbital within 24 h of capture, and karyotypes prepared from bone marrow and/or spleen cells following in vivo methodology (Patton 1967, Rickart et al. 1989). Material from freshly killed animals caught in snap traps was processed in vitro (Rickart et al. 1998). Cells were processed and fixed in the field, and standard (non-differentially stained) karyotypes were prepared from stored cell suspensions. Preparations of silver-stained nucleolus organizer regions (Ag-NORs; Howell & Black 1980) and G-banded chromosomes (Seabright 1971) were made for some taxa. A minimum of 10 chromosomal spreads was examined from each preparation. Chromosome terminology follows Rickart and Musser (1993). As used herein, fundamental number (FN) refers to the total number of chromosome arms in the female karyotype (including those of sex chromosomes). Species nomenclature follows Heaney et al. (1998).

Voucher specimens were prepared as skins with partial skeletons, complete skeletons, or preserved in fluid, and are deposited in the Field Museum of Natural History, Chicago, IL (FMNH), the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM), and the Philippine National Museum, Manila (PNM). Microscope slides of chromosomal preparations and photomicrograph negatives cross-referenced to cataloged voucher specimens are housed at the Utah Museum of Natural History, University of Utah, Salt Lake City.

Specimens Examined

Podogymnura truei Mearns, 1905.—Mindanao Island, Bukidnon Province, Mount Kitanglad Range, 16.5 km S, 4 km E Camp Phillips, elev. 1900 m, 8°10′30″N, 124°51′E, 2 males (FMNH 147793, 147798).

Crocidura beatus Miller, 1910.—Leyte Island, Leyte Province, Mount Pangasugan, 10 km N, 4.5 km E Baybay, elev. 950 m, 10°47′N, 124°50′E, 1 male (USNM 457984).

Crocidura grayi Dobson, 1890.—Luzon Island, Camarines Sur Province, Mount Isarog, 4 km N, 22 km E Naga, elev. 1750 m, 13°40′N, 123°22′E, 1 female, 1 male (USNM 573607, 573617).

Suncus murinus (Linnaeus, 1766).—Negros Island, Negros Oriental Province, Silliman Farm, Dumaguete, elev. 5 m, 09°18′N, 123°18′E, 2 males (USNM 457996, 457997); Mount Guinsayawan, 3 km N, 17 km W Dumaguete, elev. 1470 m, 9°22′N, 123°9′E, 1 female, 1 male (USNM 458970, 458972).

Cynocephalus volans (Linnaeus, 1758).—Leyte Island, Leyte Province, 7 km N Baybay, elev. 10 m, 10°45′N, 124°47′30″E, 1 female (USNM 458982).

Tarsius syrichta (Linnaeus, 1758).—Leyte Island, Leyte Province, 7 km N, 1.5 km E Baybay, elev. 50 m, 10°45′N, 124°48′E, 1 male (PNM specimen, EAR field number 1441); Mount Pangasugan, 10.2 km N, 2.2 km E Baybay, elev. 320 m, 10°46′N, 124°49′E, 1 male (USNM 459818); Mount Pangasugan, 8.5 km N, 2.5 km E Baybay, elev. 500 m, 10°45′30″N, 124°49′30″E, 1 male (USNM 458723).

Sundasciurus philippinensis (Waterhouse, 1839).—Biliran Island, Leyte Province, 5 km N, 10 km E Naval, elev. 850 m, 11°36′N, 124°29′E, 1 male (USNM 459821).

Paradoxurus hermaphroditus (Pallas, 1777).—Leyte Island, Leyte Province, 7 km N, 1.5 km E Baybay, elev. 50 m, 10°45′N, 124°48′E, 1 male (USNM 458891); Mount Pangasugan, 10 km N, 2 km E Baybay, elev. 300 m, 10°46′N, 124°49′E, 1 male (USNM 459999).

Viverra tangalunga Gray, 1832.—Leyte Island, Leyte Province, Mount Pangasugan, 10 km N, 2 km E Baybay, elev. 300 m, 10°46′N, 124°49′E, 1 male (USNM 460000).

Results

Order Insectivora
Family Erinaceidae

Podogymnura truei. 2N = 40, FN = 76, Fig. 1A.—The karyotype of the Mindanao gymnure includes 11 pairs of small to large-sized metacentric or submetacentric autosomes, 6 pairs of medium-sized subtelocentric autosomes, and 2 pairs of small or medium-sized telocentric autosomes. The small X chromosome is submetacentric, and the minute Y chromosome appears to be telocentric.

Family Soricidae

Crocidura grayi. 2N = 38, FN = 58, Fig. 1B.—The karyotype of the Luzon shrew includes 4 pairs of small to medium-sized submetacentric autosomes, 5 pairs of small to large-sized subtelocentric autosomes, and 9 pairs of small to large-sized telocentric autosomes. The X chromosome is medium-sized and subtelocentric, and the small Y chromosome is submetacentric.

Crocidura beatus. 2N = 38(?), FN = ?, not figured.—A poor quality in-vivo prep-

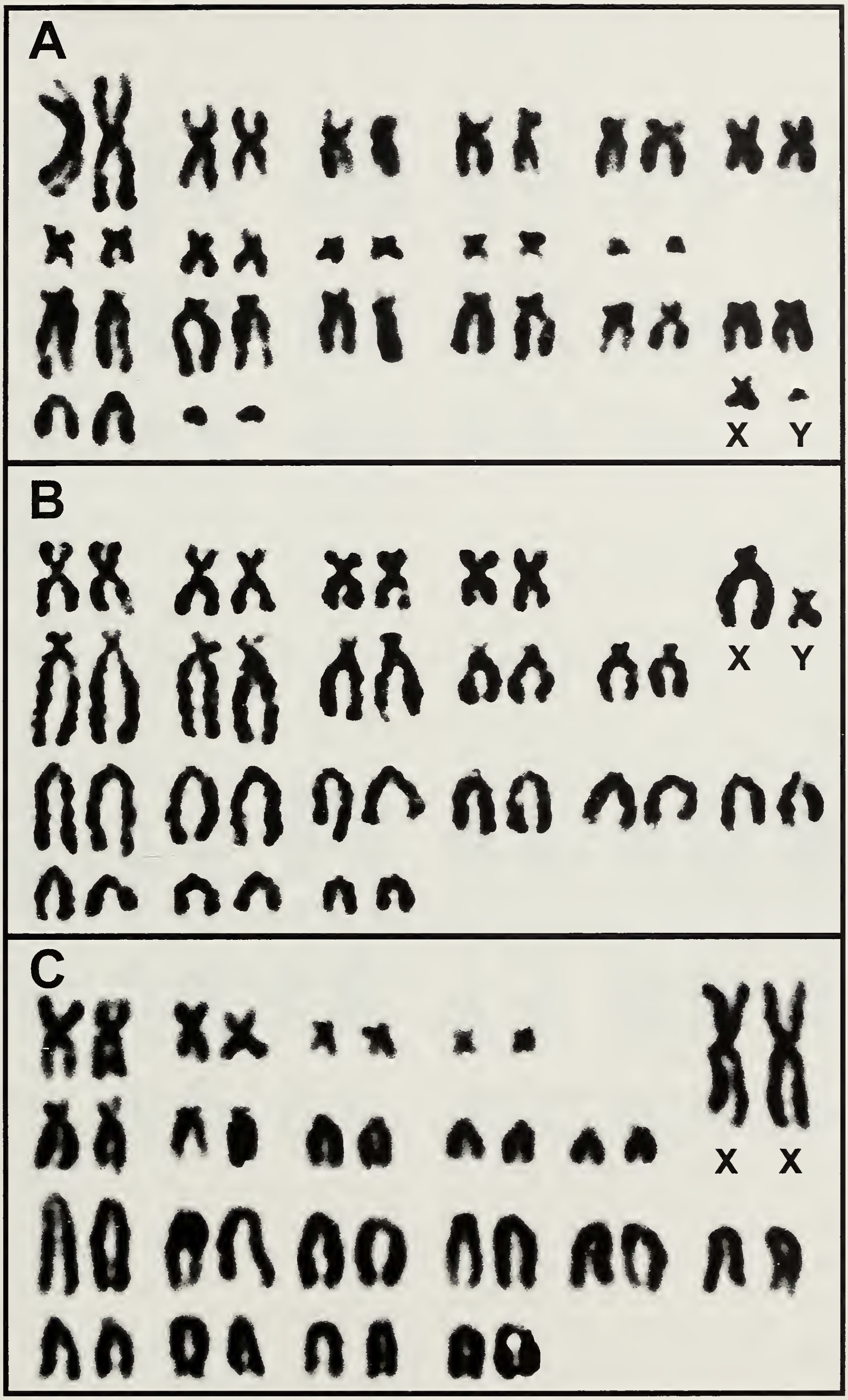

Fig. 1. Karyotypes of: A) *Podogymnura truei,* male (FMNH 147793) from in vitro preparation, 2N = 40; B) *Crocidura grayi,* male (USNM 573617), 2N = 38; C) *Suncus murinus,* female (USNM 458970), 2N = 40.

aration yielded preliminary information on the chromosomes of this species which is endemic to the Mindanao faunal region. The modal chromosome count from multiple spreads was 38, indicating a karyotype similar to that of *C. grayi* (Fig. 1B).

Suncus murinus. 2N = 40, FN = 60, Fig. 1C.—Specimens of the Asian house shrew from Negros Island have a karyotype that includes 4 pairs of small to large-sized submetacentric autosomes, 5 pairs of small to medium-sized subtelocentric autosomes, and 10 pairs of medium to large-sized telocentric autosomes. Both the X and Y chromosomes are submetacentric.

Order Dermoptera
Family Cynocephalidae

Cynocephalus volans. 2N = 38, FN = 40, Fig. 2.—The standard karyotype of a female Philippine flying lemur from Leyte Island includes 18 pairs of small to large-sized telocentric autosomes and a pair of medium-sized submetacentric X chromosomes. A G-banded preparation reveals G-positive bands on the nine largest autosomes. The X chromosome is largely G-positive. Ag-NORs are located terminally on the smallest telocentric autosomes.

Order Primates
Family Tarsiidae

Tarsius syrichta. 2N = 80, FN = 94, Fig. 3A.—Karyotypes of male Philippine tarsiers from Leyte Island include 6 pairs of small to large-sized metacentric or submetacentric autosomes and 33 pairs of small to large-sized telocentric autosomes. The submetacentric X and minute Y chromosomes are, respectively, the largest and smallest elements in the karyotype.

Order Rodentia
Family Sciuridae

Sundasciurus philippinensis. 2N = 38, FN = 72, Fig. 3B.—The karyotype of a male Philippine tree squirrel from Biliran Island includes 9 pairs of metacentric or submetacentric autosomes, 7 pairs of subtelocentric autosomes, and 2 pairs of small telocentric autosomes. The medium-sized X chromosome is submetacentric and the minute Y chromosome appears to be telocentric.

Order Carnivora
Family Viverridae

Paradoxurus hermaphroditus. 2N = 42, FN = 72, Fig. 4A.—Specimens of the common palm civet from Leyte Island have a karyotype that includes 8 pairs of small to large-sized metacentric or submetacentric autosomes, 6 pairs of small to large-sized subtelocentric autosomes, and 6 pairs of small to medium-sized telocentric autosomes. The medium-sized X chromosome is submetacentric, and the small Y chromosome is telocentric.

Viverra tangalunga. 2N = 36, FN = 64, Fig. 4B.—The karyotype of a male Malay civet from Leyte Island includes 7 pairs of small to large-sized metacentric or submetacentric autosomes, 6 pairs of small to large-sized subtelocentric autosomes, and 4 pairs of small telocentric autosomes. The X chromosome is large and submetacentric and the small Y chromosome is telocentric.

Discussion

The 2N = 40, FN = 76 karyotype of *Podogymnura truei* (Fig. 1A) is the first reported for the gymnure subfamily Hylomyinae. It differs substantially from those of hedgehogs (subfamily Erinaceinae) which have relatively uniform karyotypes of 2N = 48, FN = 90–96 and X chromosomes that are substantially larger than that of *P. truei* (Gropp 1969, Bhatnagar & El-Azawi 1978, Hübner et al. 1991, Reumer & Meylan 1986).

The widespread genus *Crocidura* displays extensive interspecific chromosomal variation (Maddalena & Ruedi 1994, Zima et al. 1998). There are seven species of *Crocidura* in the Philippines (Heaney &

Fig. 2. Karyotypes of *Cynocephalus volans,* female (USNM 458982), 2N = 38: A) standard, inset of Ag-NOR sites; B) G-banded.

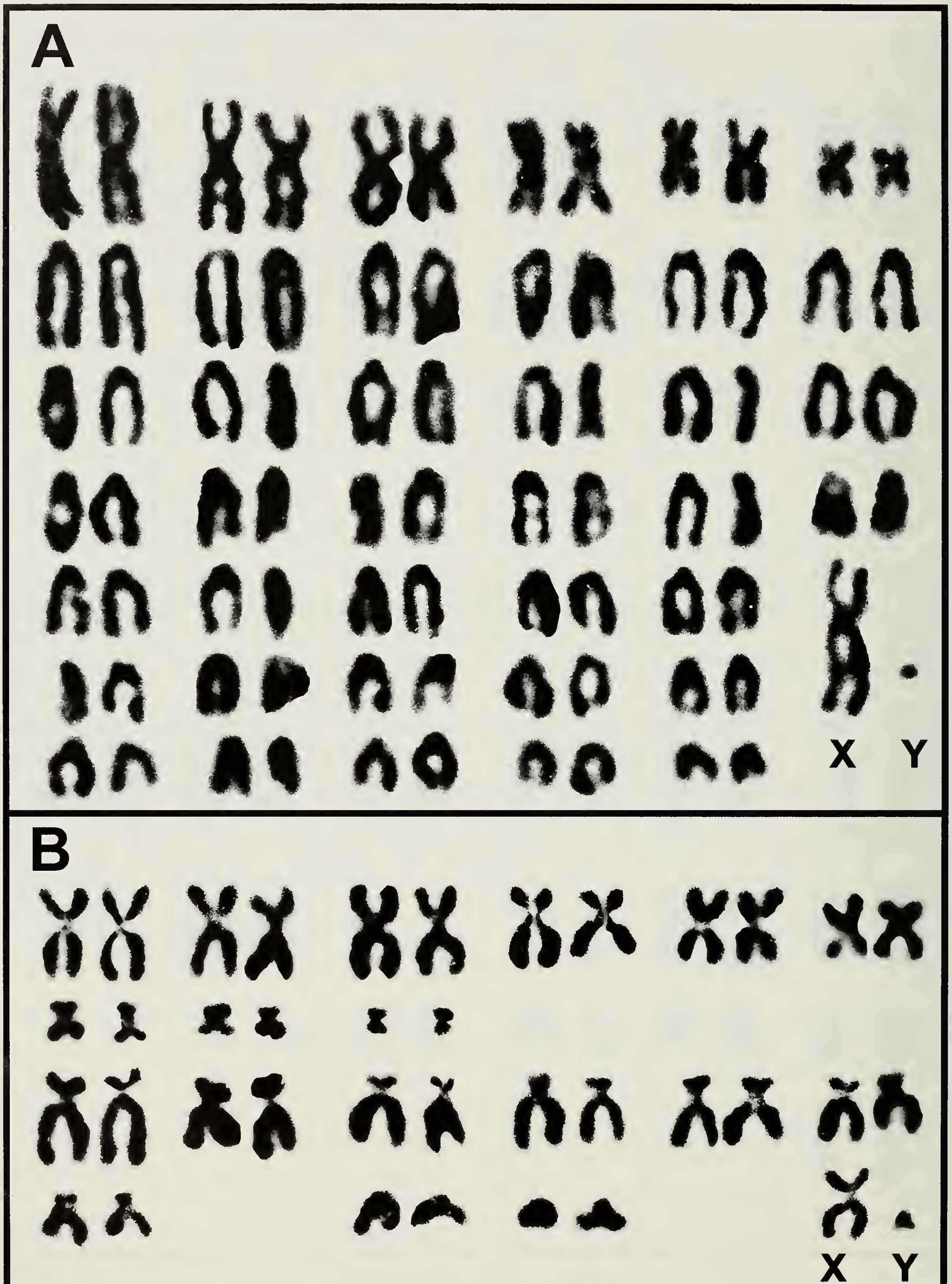

Fig. 3. Karyotypes of: A) *Tarsius syrichta,* male (EAR 1441), 2N = 80; B) *Sundasciurus philippinensis,* male (USNM 459821), 2N = 38.

Fig. 4. Karyotypes of: A) *Paradoxurus hermaphroditus,* male (USNM 458891), 2N = 42; B) *Viverra tangalunga* male (USNM 460000), 2N = 36.

Ruedi 1994) of which two have been karyotyped (this study). The 2N = 38, FN = 58 karyotype of *C. grayi* (Fig. 1B) resembles those of several species with 2N = 38, FN = 54–58 from islands of the Sunda Shelf and from Sulewesi (Ruedi & Vogel 1995). It also is similar to the presumed ancestral arrangement for *Crocidura* (Maddalena & Ruedi 1994). The apparent similarity in the karyotypes of *C. grayi* and *C. beatus* is consistent with morphometric and allozyme data that place these species as sister-taxa (Heaney & Ruedi 1994). The limited data available suggest that the diversification of Philippine *Crocidura* has not involved major chromosomal rearrangements of the sort seen for members of the genus in Sulewesi (Ruedi & Vogel 1995), or for Philippine rodents of the genus *Apomys* (Rickart & Musser 1993, Rickart & Heaney 2002).

Suncus murinus is a chromosomally polymorphic species (2N = 30–40) found throughout much of southeast Asia (Yoshida 1985, Zima et al. 1998). It occurs throughout the Philippines as a non-native commensal (Heaney et al. 1998), and on Negros Island, it also is naturalized and abundant in primary forest habitat (Heaney et al. 1989). Both commensal and naturalized animals from Negros have identical karyotypes of 2N = 40, FN = 60 (Fig. 1C). This same arrangement has been reported for specimens from much of southeast Asia (Zima et al. 1998). Medina and Leonard (1977) reported a karyotype of 2N = 40, FN = 54 for *S. luzoniensis* (a synonym of *S. murinus*) from Luzon Island. The difference in FN compared to the Negros specimens most likely reflects variable assessment of minute secondary arms on subtelocentric autosomes.

The 2N = 38, FN = 40 karyotype of *Cynocephalus volans* (Fig. 2), one of two members of the mammalian order Dermoptera, is reported here for the first time. This also corrects an erroneous report by Hsu and Benirschke (1973). They published identical karyotypes of 2N = 56, FN = 72 for a specimen of *Galeopterus variegatus* from Malaysia and for an animal at the Lincoln Park Zoo, Chicago, originally identified as *C. volans.* After the latter died, it was sent to the Field Museum where it was accessioned and correctly identified as *Galeopterus* (FMNH 60308; W. Stanley, pers. comm.). The two dermopterans have substantially different karyotypes. *Cynocephalus* lacks nine pairs of autosomes present in *Galeopterus,* including seven pairs of small to large-sized biarmed chromosomes, and the X chromosome of the former is submetacentric whereas that of the latter is metacentric (Fig. 2; Hsu & Benirschke 1973). The Ag-NORs of *Cynocephalus* are located on the smallest autosomal pair (Fig. 2). In *Galeopterus,* this same pair bears secondary constrictions (Hsu & Benirschke 1973). This chromosomal distinctiveness is in accord with the substantial morphological and ecological differences that suggest ancient divergence of the two species and supports their placement in separate genera (Stafford & Szalay 2000).

The karyotype of *Tarsius syrichta* from Leyte Island (Fig. 3A) is identical to those previously reported for specimens from Mindanao (Boer & Boer-Van der Vlist 1973, Dutrillaux & Rumpler 1988). *Tarsius bancanus* also has 2N = 80, FN = 94 (Klinger 1963), but its karyotype differs from that of *T. syrichta* in the size and relative arm lengths of several of the biarmed autosomes. *Tarsius dianae* from central Sulawesi is the only other tarsier that has been karyotyped. Its arrangement of 2N = 46, FN = 82 (Niemitz et al. 1991) differs from those of *T. syrichta* and *T. bancanus* by multiple Robertsonian and non-Robertsonian events. Chromosomal data support phylogenetic hypotheses based on comparative morphology and behavior that associate the Philippine and Sundaic species (*T. syrichta* and *T. bancanus*) as relatively specialized forms separate from the three species of Sulawesian tarsiers (Niemitz 1977, Musser & Dagosto 1987, Dagosto et al. 2001).

The 2N = 38, FN = 72 karyotype of *Sundasciurus philippinensis* (Fig. 3B) is reported here for the first time. It is identical to that of *S. jentinki,* the only other member of the genus that has been karyotyped (Harada & Kobayashi 1980). Among callosciurine squirrels, *Dremomys rufigenis* and *Callosciurus albescens* also share this arrangement (Nadler & Hoffmann 1970, Harada & Kobayashi 1980), and several other species of *Callosciurus* have karyotypes of 2N = 40, FN = 70–74 that differ only slightly from that of *S. philippinensis* (Nadler et al. 1975, Yong Hoi-Sen et al. 1975, Oshida & Yoshida 1999). The available data suggest that callosciurines are chromosomally conservative.

A karyotype of 2N = 42, FN = 78 was reported previously for *Paradoxurus hermaphroditus* from India (Ray-Chaudhuri et al. 1966). The karyotype of Philippine specimens (Fig. 4A) is similar, but appears to have fewer subtelocentric and more telocentric elements (FN = 72). In other respects, the two karyotypes are identical.

The 2N = 36, FN = 64 karyotype of

Viverra tangalunga (Fig. 4B) is the first reported for this widespread southeast Asian species. *Viverra zibetha,* the only other member of this genus that has been examined has a substantially different karyotype of 2N = 38 and FN = 68 (Pathak 1971). Among members of the subfamily Viverrinae that have been examined, *Viverricula indica* is the only species with 2N = 36 (Wurster & Benirschke 1968). However, *Viverra tangalunga* has more telocentric and fewer subtelocentric autosomes, and a significantly smaller Y chromosome than does *Viverricula.*

Interpretation of these chromosome data is limited, in some cases, by the lack of comparative information on related taxa. Nonetheless, some general patterns of variation are apparent. Members of the endemic genera *Podogymnura* and *Cynocephalus* have karyotypes that differ substantially from those of related taxa. In contrast, endemic species of *Tarsius, Crocidura,* and *Sundasciurus,* and the widespread species *Suncus murinus* and *Paradoxurus hermaphroditus* have karyotypes that are similar, or identical, to those of closely related species or conspecifics occurring elsewhere in Asia. These results mirror patterns of chromosomal variation documented for Philippine bats and murid rodents (Rickart et al. 1999, Rickart & Heaney 2002). Most endemic taxa have karyotypes that are unique compared to relatives occurring outside of the Philippines. Some widespread species exhibit chromosomal polymorphism, in which Philippine populations have unique karyotypes. The general pattern is one of chromosomal rearrangement occurring as a result of isolation. The degree to which this pattern is expressed appears to be largely a function of how long a particular group has been present within the archipelago.

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